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ON VARIATION IN AN ANTHROPOCHOROUS SPECIES
OF THE ORIENTAL EARTHWORM GENUS
PHERETIMA KINBERG 1866¹

BY

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A very considerable mass of data *re* variation must be procured before "museum" or "typological" species in the classical system of the Oligochaeta can be considered good according to canons of the "New Systematics." The labors of Dr. Y. Kondo, his family and friends, as well as of herpetologist A. J. Loveridge (in his retirement), now have provided good series, from Hawaii and St. Helena respectively, of one species for comparison with lots from the United States, Mexico, Guatemala, Salvador, Bermuda, Brazil, Argentina, Madeira, South Africa, Pakistan, India, and Singapore.

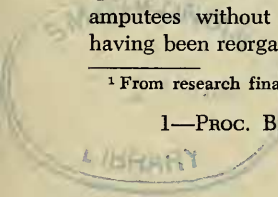
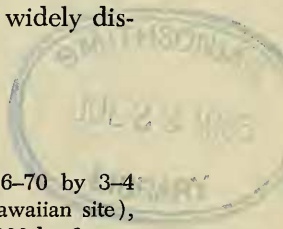
The species herein considered is not too inappropriately named *hawayana* as it now appears, from Dr. Kondo's numerous collections of the last six years, to be the most widely distributed and common earthworm in Hawaii.

Pheretima hawayana (Rosa, 1891)

EXTERNAL CHARACTERISTICS

Size, of strongly contracted, unamputated specimens, 56-70 by 3-4 mm. (1 Hawaiian site), 110-156 by 5-6 mm. (another Hawaiian site), of relaxed specimens from Los Angeles and Singapore 165-200 by 6 mm. Segment number of individuals with a normal tail, *i.e.*, without regeneration or amputation, was 70-101 (*cf.* Table 1). The range is only slightly greater than that of previous records (*cf.* PR column, Table 1). However, Table 1 shows more than three-fourths of the specimens recently counted had 91-98 segments. Some of the tabulated specimens with fewer than 87 metameres may have been old posterior amputees without regeneration but with the present terminal region having been reorganized so as to look almost, if not exactly, like a normal

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2 *Proceedings of the Biological Society of Washington*TABLE 1.—Segment number in *Pheretima hawayana* (Rosa, 1891)

Number of segments	Number of specimens										Totals
	PR	N.A.	Saint H.	Singapore	Hawaii						
					A	B	C	D	E	F	
70					2			1			3
71	1				1			1			3
72											
73					3		1				4
74					1						1
75		1				1		1			3
76					1	1		4			6
77			2			1		3			6
78	1	1		1		2		4	1	1	11
79		1		1		1	1	6	1	1	12
80						1		4	1		6
81			1	1		1		12			15
82						1	1	8			10
83	1					1		9	1	2	14
84		1				1	1	9	1		13
85		1					1	4	1		8
86	1		1					3		1	6
87			1	1	1		1	3			7
88	2	1	1					10			14
89		2	1	1			1	6			11
90	1	1	2				1	11	5	4	25
91		1	1					20	7	8	37
92	1	2	3					34	6	5	51
93	1	6	8	2			4	58	7	12	98
94	1	3	9	4			2	59	11	12	101
95	1	2	7	4			4	57	8	11	94
96	1	1	6	5			1	47	4	5	70
97	1	1	4	1			1	22	1	1	32
98			1	1			2	15	1		20
99				1				7	2		10
100											
101								1			1
Totals	13	25	48	23	10	12	21	419	58	63	692

PR Previous records. Information as to number of counts rarely was published. Records such as 71-94 and 88-95 accordingly are tabulated above as 71 once, 94 once, 88 once, 95 once.

N.A. North America.

Saint H. Saint Helena.

adult tail. Usually the last 2-6 segments of unamputated individuals are quite small, with few or no visible setae but with the color of the more anterior metameres.

Color, various, brownish, reddish brown, yellowish brown, reddish, almost purple, slate, greyish, bright red (almost only in young juveniles). Total albinism was not seen but an Indian series from 5,500-6,000 feet, at Gangtok, Sikkim, contained one individual in which pigmentation gradually disappeared in the region of xvii-xxviii. From xxix posteriorly the soma was of an unusually clear white. Iridescence occasionally is marked and of a brilliant green but is especially obvious on worms with cuticle more or less loosened. Prostomium, epilobous, tongue open (354 specimens). Setal size increases from ii through vi, especially ventrally, as the distance between follicle apertures increases. Size is much smaller in vii though somewhat larger, at least ventrally, than in viii and posteriorly where intersetal distances are smaller. Setal counts on a St. Helena worm of 91 segments were as follows; 20/ii, 20/iii, 40/viii, 40/xii, 53/xx, 50/xxx, 51/xl, 49/l, 59/lx, 56/lxx, 47/lxxix, 45/lxxx, 49/lxxxi. Previous records, 40 in spermathecal segments, 60-64 in postclitellar segments (Hawaii), 56/xii (Yunnan), 17-21/iii, 36-40/viii, 44-49/xii, 48-56/xx (Burma). Determining limits of variation in number per segment is complicated by the absence of information about shedding (which is involved) as well as about any correlation of number with soma size. Number per segment seems to increase gradually to somewhere in the region of xii-xxv and then near the hindend gradually decreases. Setae almost always were recognizable in xvi of St. Helena and Hawaii worms. The number, 3 (1 specimen), 4 (3, including 1 Mexican), 6 (4), 7 (3), 8 (5), 9 (8), 10 (8), 11 (4), 12 (6), 13 (5), 14 (5), 15 (1), 16 (5), 17 (6), 18 (6), 19 (2), 28 (1, with but slight modification of clitellar epidermis), 30 (1), complete ring (1). Some of those larger numbers might have become smaller by the time clitellar tumescence was maximal. Setae were recognized in xiv more often than in xv but occasionally were present in both. Whether setae are retained in follicles of clitellar segments after occlusion of the follicle apertures is unknown. Number of setae between male porophores in xviii, 11 (2 specimens), 13 (5), 14 (6), 15 (11), 16 (9), 17 (3), 18 (5), 19 (2), 21 (1), previously recorded 10-15 (Burma).

First dorsal pore, function determined by bending the worm slightly toward ventral side so as to force fluid out of coelomic cavity, usually

←

- A Probably old or obviously recent amputees.
- B Possibly amputees?
- C Very small unamputated juveniles from a locality at which only *hawayana* was obtained.
- D Others, including late juvenile, acitellate and clitellate individuals presumably unamputated and without regeneration.
- E Juvenile, 1964, only those with tail regenerates screened out.
- F Mature, 1964, only those with tail regenerates screened out. The 1964 series were from several islands.

TABLE 2.—Location of first dorsal pore in *P. hawayana*

Intersegmental furrows	Number of specimens from		
	Saint Helena	Singapore	Hawaii
9/10			2
(9/10?) 10/11			20
10/11	27	22	359
(10/11?) 11/12	1		16
(9/10, 10/11?) 11/12			3
11/12	1		4
(10/11, 11/12?) 12/13			1

at 10/11. Pore-like spots from which no fluid emerged are indicated in Table 2 by question marks. As in case of the prostomium and other structures, characters were not recorded for every specimen, especially after lack of significant variation became obvious.

The clitellum never seemed to extend all the way through the usual three segments but is much more likely to reach 13/14 than 16/17. Nevertheless, the dorsal pore at 13/14 always seemed to be functional as did the pore at 16/17. Intersegmental furrows 14/15, 15/16 are obliterated and the dorsal pores at those two levels are occluded. Earliest regular dehiscence of setae during growth appears to be near mV in xiv.

Spermathecal pores often are quite unrecognizable in strongly contracted and well-preserved material. Variation in number of spermathecae, accordingly may be greater than was determined from the dissections. The pores, always minute and superficial, always are median to mL and perhaps are usually about 1/3 C apart. The female pore always was minute and superficial and probably is uniformly so through the genus, the family Megascolecidae and other megadrile families with the single exception of the Eudrilidae. A single pore, in xiv of *hawayana*, always was median. A pair of female pores, in xiv, was present on two worms, one each from Mexico and Hawaii. Male pores also always were minute and superficial but usually were closed (like the female pore), and in that condition sites were not certainly distinguishable. Male porophores usually were somewhat larger than adjacent genital markings but on several Singapore specimens were almost exactly of the same size. Anlage of the male porophores become recognizable during growth before those of the genital markings.

Genital markings are rather small, circular areas, distinctly delimited peripherally and often with a discoidal appearance. A slightly raised marginal band is opaque and a slightly concave central area of contracted worms is greyish translucent. Such a central area was lacking on relaxed specimens. Instead there was recognizable, just inside the marginal band, a circle of 8–12 greyish translucent dots, each of which may show site of a pore of one unit of the composite gland that is associated with

TABLE 3.—Number and location of preclitellar genital markings in *Pheretima hawayana*

Segments	Number of specimens from					Totals
	Burma PR	North America	St. Helena	Singapore	Hawaii	
v-vii		1				1
vi-vii					2	2
vii	4	7	4	10	169	194
vii-viii	2				11	13
viii	6		1	3	9	19

each marking. With one exception (a St. Helena worm with a pair of markings in xvii) postclitellar markings were confined to xviii. All markings were postsetal. Markings were absent in 10 specimens including 4 from St. Helena and 6 from Hawaii. Preclitellar markings are median to longitudinal meridians of the spermathecal pores by distances equal to 2-4 nearby intersetal intervals and are closer to the intersegmental furrows (posterior) than to the segmental equators. Postclitellar markings of xviii always are in a region just posteromedian to the male porophore. As many as nine postclitellar markings were previously reported from Bermuda, 10 from Burma, 12 from Honolulu as well as from a Kurseong site in the Himalayas but more than 12 of the tubercles only now are recorded and from Hawaii alone. The larger numbers are not as yet regarded as peculiar to Hawaii for only from those islands were enough specimens examined to reveal the probable range of variation, 0-21. Markings are in one or more transverse rows of two to six but the row arrangement is less obvious when numbers are larger. Positioning often is the same on both sides of xviii even when the numbers are different. Determining just which markings of one side are lacking on the other, often is possible.

INTERNAL ANATOMY

Pigment, always reddish brown and in the circular muscle layer, often present in the special longitudinal band at mD, was dense in the preclitellar dorsum and more sparse posteriorly. The longitudinal muscle band at mD ends anteriorly in x. Brain and commissures were left in iii by a transverse section exactly along $3/4$ if the buccal cavity was completely retracted. That cavity can be everted until the protrusion is longer than combined lengths of i-ii. When so everted the brain usually was left in ii, but posteriorly, by a transverse section exactly along $2/3$. The brain was however left in iii anteriorly or posteriorly of two worms with marked buccal protrusion.

Variation in thickness of certain anterior septa is difficult to estimate and the more obvious differences seem to be associated with contracted-relaxed states of the soma. Septa 5/6-7/8, 10/11-13/14, certainly are

TABLE 4.—Number of postclitellar markings in *P. hawayana*

Number of markings on left and right sides	Number of specimens from					Totals
	Burma PR	North America	Saint Helena	Singapore	Hawaii	
0-0			4		6	10
0-1	5		1	2	4	12
1-0					5	5
0-2			1		1	2
2-0					2	2
0-3					1	1
3-0					1	1
5-0					1	1
1-1		13	8	16	28	65
1-2	3	2	8		23	36
2-1	1		9	5	14	29
1-3					4	4
3-1					4	4
4-1					1	1
2-2	9	9	8	8	98	132
2-3	2		4		28	34
3-2			1		26	27
2-4					8	8
4-2					3	3
6-2					1	1
3-3			5	1	54	60
3-4	1	1			24	26
4-3			2		18	20

thickened and opaque, probably with some gradual decrease posteriorly through the last four. Septum 9/10 always was aborted except perhaps for some ventral rudiment in the wall of the anterior testis sac. Septum 8/9 usually appeared to be aborted except for occasional persistence of a ventral rudiment, but in one specimen was complete though transparent. Such a delicate membrane can be ruptured so as to leave only a ventral rudiment merely by pinning back the body wall to permit examination of internal organization. As in all other pheretimas, when 8/9 is present the gizzard was confined to viii.

No variation of importance was noticed in characters of gizzard, esophagus. The intestinal origin always was in xv but sometimes the portion in xv had been drawn back into the interior of the gut in xvi so as to produce an appearance of the intestine beginning in xvi. When so withdrawn, determination of the origin can be difficult or even impossible if preservation is poor. An intestinal caecum was lacking in a single worm but in several others one of the caeca at first inspection appeared to be absent because it had been completely withdrawn into the interior of the gut. Recognition of the withdrawal could be very

TABLE 4.—*Continued*

Number of markings on left and right sides	Number of specimens from					Totals
	Burma PR	North America	Saint Helena	Singapore	Hawaii	
3-5		1			4	5
5-3					6	6
3-6					3	3
3-7					1	1
4-4			4		38	42
4-5					14	14
5-4					16	16
4-6	1				1	2
4-7					1	1
5-5		1			28	29
5-6					5	5
6-5					9	9
5-7					2	2
7-5					2	2
6-6					12	12
6-7					3	3
7-6					3	3
8-6					3	3
7-8					1	1
8-7					2	2
8-10					2	2
9-10					1	1
10-9					2	2
11-10					1	1

difficult if preservation is poor as it often is in an anterior portion of the intestinal region. An intestinal typhlosole is lacking or rudimentary and then somewhat widened but interrupted and with smaller diagonal ridges in a few segments (*cf.* Table 6) behind which no further trace is distinguishable.

Variation in the circulatory system at first appeared to be rampant and even to involve all major trunks. No trace, for instance, of a subneural trunk was recognizable in one specimen. A subneural with a pair of branches in each segment was obvious in another worm, in front of lxi, but in many individuals no vestige of the trunk was visible in front of xiii or xiv. Those and many other seeming variations are now believed to be due to the volume of blood being much smaller than that of the spaces through which it has to flow. Vessels, especially those with thin and transparent walls presumably collapse when empty and then are indistinguishable from adjacent tissues. Adding together conditions observed in various specimens enables an assumption that the subneural

TABLE 5.—Variation in number of postclitellar genital markings in *P. hawayana*

Number of markings	Number of specimens
0	10
1	17
2	68
3	66
4	140
5	63
6	71
7	46
8	56
9	33
10	30
11	15
12	16
13	6
14	3
15	3
18	2
19	3
21	1

TABLE 6.—Widening of the typhlosole in *P. hawayana*

In segments	Number of segments in the worm
41-52	94
43-56	79
45-56	81
46-54	78
46-63	94
47-64	99
48-60	89
50-59	87
50-61	94
50-64	94
52-64	98
52-65	97
53-63	95, 96
56-66	96

TABLE 7.—Location of the hearts of ix in *P. hawayana*

Sides	Number of specimens from			
	North America	Singapore	St. Helena	Hawaii
Left and right	2			3
Left only	7	8	1	57
Right only	9	9		74

really is complete from one end of the body to the other though a blood-filled condition was not seen in any single individual. The trunk always was adherent to the parietes and the anterior bifurcation was under or just in front of the subpharyngeal ganglion. The dorsal trunk usually is distended with blood and obvious throughout most of the major axis but its wall becomes thinner in front of 6/7 with the result that anterior bifurcations and connections with the ventral trunk usually are unrecognizable. Hearts of xi-xiii are believed to be always lateroesophageal though blood in the slender connectives to the dorsal trunk usually was lacking. Hearts of x, presumably esophageal as no tissue passing to the dorsal trunk was seen, were recognized because distended with blood, in 63 specimens. In others a blood-filled heart was found on one side. A distended heart without blood was recognized on several occasions. Whether hearts of x were merely unrecognizable because empty or were lacking in 25 specimens is unknown. One or the other of the always lateral hearts belonging to ix usually had aborted (*cf.* Table 8) and a similar abortion could have eliminated one or both hearts of x. Major portions of the hearts of viii always had aborted, the remaining short portions passing from the dorsal trunk to the gizzard. Hearts of vi-vii, when complete always were lateral but frequently, and most often in vi, could not be traced to the ventral trunk. Extra-esophageal trunks occasionally were seen to pass off from gut to parietes and then to run straight posteriorly into xiv and further back before turning to the subneural. Occasionally a pair of connectives, posteriorly in xiii, between supra-esophageal and subneural were recognized. Lymph glands, in especially well-preserved specimens were present from xvi posteriorly. Blood glands, believed by Stephenson (1924) to be vestigial in this species, were not always distinguishable in each of iv-vi.

Testis sacs, always ventral, usually were unpaired and often were above the nerve cord (but this character frequently was not recorded). Some of those that appeared at first glance to be paired actually were unpaired. Communication between sacs of different segments always was lacking. Seminal vesicles of juveniles always had a demarcated dorsal lobe (primary ampulla) that often was not recognized in adults. At maturity, vesicles always were soft and fairly large, usually filling all available space in coelomic cavities of xi and xii. Pseudovesicles of xiii and xiv, in juveniles so small that spermathecae had not become visible in coelomic cavities, were larger relative to soma size than in

TABLE 8.—Variation in number of normal spermathecae in *P. hawayana*

Locations of extra spermathecae	Number of specimens from		
	Burma PR	St. Helena	Hawaii
Left side of v	1		
Left and right sides of v	1		
Left side of ix		1	3
Right side of ix	4		1
Left and right sides of ix	2	1	2
Left and right sides of v, right side of ix	1		
Right side of ix (but left anterior spermatheca lacking)	1		

adults though slightly smaller than the vesicles of xi, xii. A small clump of granular brown debris occasionally was present dorsally in adults. These anomalous organs are serially homologous with the seminal vesicles of xi–xii but no one ever suggested that they were once associated, even in a very ancient past, with testes in xii and xiii. The vesicles in xiv, at various times, were said to be ovisacs but ova never were found therein. Prostates always were present and those of adults (extending through some or all of xvi–xxiv) always were in a mature and presumably functional state though what that function may be is unknown. Prostatic ducts were 3–6 mm. long, always muscular, in a hairpin bend, variously twisted or looped. Vasa deferentia always passed into the gland near the prostatic duct or into the ental end of the duct.

Ovaries always were more or less fan-shaped and at full maturity with numerous egg strings. Spermathecae were fairly large, when the ampulla was distended reaching up into contact with the dorsal parietes and filling most of the coelomic cavity in their own segments. The single diverticulum, from anterior face of duct at the parietes, always was shorter than the main axis and very rarely was shorter than the duct. A seminal chamber usually was not distinctly demarcated but is represented by an asymmetrical and gradual widening of a considerable ental portion of the diverticulum. Even when a terminal ental portion was constricted so as to have a size and shape of the *diffrigens* seminal chamber, sperm were not confined therein but were continued much further ectally as usual. Slenderness of the spermathecal duct is characteristic. Extra spermathecae were present in 10 of 465 Burmese specimens. Recognized variation in number of normal spermathecae, with two exceptions, are indicated in Table 9. Omitted individuals (2) lacked one organ, the right posterior spermatheca (Polynesia), the left anterior spermatheca (Hawaii).

Each spermatheca (whether extra or otherwise), in every specimen dissected, opened anteriorly. Sperm usually were present in seminal

chambers of extra spermathecae and white coagulum usually was present in the ampullae.

GM glands are stalked and coelomic. One such gland usually was associated with each preclitellar genital marking. Occasionally, when a genital marking was rather indistinct, glandular material seemed to be lacking at ental ends of the stalks. A gland that passes into the parietes with the spermathecal duct sometimes has been mistaken by certain authors for a spermathecal diverticulum but in each such case found in *hawayana* the stalk could be traced to a discrete marking. The gland probably is composite as the stalk seems to be so. Behind the clitellum exact correspondence between glands and markings was lacking. One worm with 3-5 glands in xviii had only 1-1 markings. Gland/GM ratio of two other worms were 2-2/1-1, 3-3/2-2. Some of the extra glands may pass to the male porophores as seems to be the case in *P. diffringens*, but in several specimens without postclitellar markings no glands were present in xviii. Glands may sometimes appear at first to be absent because bound down against the parietes.

ABNORMAL SPECIMENS

No. 1. Left spermatheca of vi adiverticulate (Burma PR).

No. 2. An adiverticulate spermatheca on right side of ix (Burma PR).

No. 3. An adiverticulate spermatheca on left side of v (Burma PR).

No. 4. Adiverticulate spermathecae on left side of v and right sides of v and ix (Burma PR).

No. 5. Ental half of diverticulum of right posterior spermatheca, bifid. Left posterior spermatheca doubled, including pores. All seminal chambers with sperm (Hawaii).

No. 6. Two pairs of spermathecae in vi. Three spermathecae on right side of vii, the medianmost adiverticulate. Two spermathecae on left side of vii, right side of viii. Two adiverticulate spermathecae on left side of viii. Spermathecal pores were not recognized but each duct passes into and through the muscular layers independently. Except as otherwise indicated each spermatheca is normal and with spermatozoal iridescence in the diverticulum (St. Helena).

No. 7. Right posterior spermatheca, with sperm in a normal diverticulum. Main axis (ental to parietes which is about of normal duct length has no indications of differentiation into duct and ampulla (Hawaii).

No. 8. The extra diverticulum of a bidiverticulate spermatheca is short but does have sperm in a spheroidal seminal chamber.

No. 9. An extra male porophore, on left side of xvii, with its own prostate. Left sperm ducts pass into anterior prostatic duct (St. Helena). The condition could have resulted from elision of a mesoblastic somite at the 16th or 17th level associated with halving of the somite at the 18th level. (Location of intestinal caeca unknown.)

No. 10. Heart of xiii, lacking.

No. 11. Seminal vesicles, lacking (St. Helena). Male funnels, without any trace of iridescence. Iridescence in spermathecae showed that copulation had been completed. The worm was male sterile and its copulatory partner clearly could have received no foreign sperm! Whether that partner could have received any of its own seems doubtful and, if not, absence of spermatozoa in the spermathecae is not always an indication that copulation had not taken place.

No. 12. Median female pores, in xiv, xv. Left male pore, in xix. Clitellum, of left side in xv-xvii. Paired pseudovesicles of xiii, xiv unusually large. A heart present in xiv on left side. Ovaries on left side, in xiii, xiv, each with a female funnel and oviduct. Intestinal origin of left side slightly more posterior than on the right side but both intestinal caeca appear to arise in xxvii. Abnormal conditions obviously arose from halving of the left mesoblastic somite at the 13th level. However, the left intestinal caecum presumably should be one segment behind the right. (Except as otherwise indicated, the specimen was normal. Hawaii.)

Presence of a pair of normal spermathecae in ix certainly represents a reversion to a more or less distant ancestral stage and suggests derivation of *hawayana* from an octothecal form with spermathecal pores at 5/6-8/9.

Presence of a pair of normal spermathecae in v with or without a pair in ix can be regarded in a sense as prophetic as well as indicative of ways that octothecal species with pores at 4/5-7/8 and decathecal species with pores at 4/5-8/9 may have arisen. Evolution accordingly may proceed not only by addition of a pair of organs at one or the other end of a series but also by simultaneous addition of a pair at each end. In that latter way a decathecal battery presumably could have arisen in *Pheretima* only after a previous deletion of an extremely ancient pair in ix.

Metameric abnormality. In the first 20 segments the only anomalies found were spirals: involving ii-iii (1 specimen), iv-vii (1), xvii-xix (1). Anomalies, of the usual kinds, in the region behind xx were recorded but only during segment counting and only on the side on which the count was made. Too many would have been overlooked to warrant discussion of frequency.

REGENERATION

Cephalic. No. 1. Amputation of or damage to the anterior end, left this worm with a peristomium much longer than usual. Ventrally there were several setae perhaps retained from the original second segment, though no vestige of an intersegmental furrow was recognized anywhere in the peristomium. If that buccal region is considered to be i, all organs are one segment in front of their normal location.

No. 2. A head regenerate of four normal segments, at 4/5.

No. 3. After anterior amputation at 13/14 an imperforate cicatrix was formed without regeneration.

TABLE 9.—Number of segments in tail regenerates of *P. hayaryana*

Level of regeneration	Number of segments in regenerate
49/50	14 PR
51/52	11
52/53	12, 20
53/54	17
55/56	17, 10, 10
58/59	19, 22
59/60	13, 17
61/62	21
62/63	17
63/64	9 PR
64/65	11
68/69	6(#), 7
67/68	12
71/72	5
73/74	4
74/75	2
75/76	8
76/77	4-6(?)
78/79	5, 6, 7
79/80	5
82/83	3
84/85	3, 5, 5
85/86	4
89/90	5

(#) Metameric abnormality in the regenerate.

(?) Metameric abnormalities.

PR Previous record. The regenerate at 49/50 with metameric anomalies proximally.

No. 4. After anterior amputation at an unknown level behind 18/19 an imperforate cicatrix was formed without regeneration.

Caudal. Metamerically segmented tail regenerates were found at various levels from 51/52 posteriorly. The data in Tables 10 and 1 suggest that tail regeneration is hypomeric regardless of level but that number of segments does decrease as level of amputation moves posteriorly. The hypomery is much less near the hindend.

Metamerically undifferentiated tail regenerates were present, one each, at 39/40, 45/46, 51/52, 52/53, 80/81, 83/84, 85/86. Some, including one at 51/52, seemed likely to become pygomeres with demarcation from substrate by an intersegmental furrow. Others, including one at 85/86, were somewhat larger and looked as if further development might have allowed some metameric differentiation. A regenerate of 16 segments may have been present at 57/58 as behind that level segments

abruptly became much smaller. However, no difference in pigmentation was recognized behind 57/58. The last five segments of six worms probably were regenerated but are excluded as difference of pigmentation from substrate could not have been recognized because of alcoholic preservation.

Reorganization, in the case of regeneration at 85/86, had resulted in the last substrate segment becoming much narrower and darker but no shorter. Almost all of the setae had been lost.

After posterior amputation at 39/40 and at 40/41, two worms (Gangtok) had formed an imperforate cicatrix without regeneration. Seven of 70 Gangtok adults were unregenerate posterior amputees.

The last two to six segments of most unamputated and mature worms, it should be here emphasized, are quite small, with few or no setae visible and except for presence of pigment looking somewhat like tail regenerates.

REPRODUCTION

Male funnels and spermathecal seminal chambers of clitellate individuals usually were iridescent. As sperm are exchanged during copulation, reproduction is assumed to be biparental. Further support for such an assumption is provided by the rarity, in 1,000+ specimens, of those organ deletions that are so characteristic of megadrile parthenogenesis. Moreover, presence of sperm on male funnels and in spermathecae was so general, in the many specimens studied, that option of parthenogenesis seems unlikely. Condition of seminal vesicles and of the prostates at maturity, except for one individual, was compatible with biparental reproduction. Finally, abnormalities that were encountered were mostly of sorts less likely to characterize uniparental polymorphism.

Spermathecal ampullae of sexual worms are distended by a material that is white and flocculent. Ampullae of postsexual individuals contain, after preservation, a transparent jell (pinkish or colorless) or a watery fluid or are empty, presumably showing different stages in lysis and absorption of the material of unknown function.

Sperm were present on male funnels and in spermathecae of a Singapore worm that had no trace of a clitellum. Spermathecal ampullae were empty but their content may have been absorbed during regeneration of an 11-segment tail regenerate at 64/65. Iridescence of spermathecal seminal chambers and distention of spermathecal ampullae by the white material was noted in specimens (from North America, Hawaii, St. Helena, and Singapore) that had been recorded from external inspection as late juvenile or early adult. Those specimens showed no indication of postsexual regression such as shrunken seminal vesicles or presence of brown debris in the vesicles. On the contrary, intersegmental furrows 14/15-15/16 were obvious or rather faint (an early stage of obliteration?), setal circles of xiv-xvi were uninterrupted and dorsal pores at 14/15 and 15/16 still were functional. Cuts through the body wall of xiv-xvi revealed no macroscopically recognizable epidermal

tumescence. Seminal vesicles as well as testis sacs were distended and without brown debris.

Unless individuals of *hawayana* are able to eliminate all other evidence of previous sexuality except the spermatozoal iridescence on their male funnels and in their seminal chambers, maturation and exchange of sperm do take place prior to appearance of the clitellum.

Conditions also indicative of preclitellate copulation, have been seen in other species of *Pheretima* as well as in individuals of other genera and families. Stigmata of postsexual regression still were recognizable in worms of various species examined soon after emergence from a rest period. No evidence has been found in the literature to indicate that megadriles can eliminate all traces of previous sexuality during a period of reproductive inactivity.

Nevertheless, all copulating earthworms seen by the author were clitellate and reports of all special studies of megadrile copulation record the participating individuals as clitellate.

PARASITES

An isolated cyst here and there, sometimes only one, was present in the nerve cord of a very few specimens. Cysts were numerous enough in three worms to interrupt neural continuity at one or more levels though no indication of that condition was recognizable externally. A few individuals had parietal cysts. Coelomic nematodes were not found. No search was made for macroscopically unrecognizable organisms—inhabitants of the seminal vesicles (at least) already had been studied at several localities and still are under investigation elsewhere. Information regarding the cyst-producing organisms may eventually be published by some of those to whom material has been sent.

Most of the individuals that were dissected either had not been exposed to the massive infestations so common in other taxa—and more particularly in parthenogenetic morphs of certain pheretimas—or else had been much more resistant.

DISCUSSION

A thousand and more specimens of *P. hawayana* were examined by the author. Each individual that showed, in the first 20 segments, any externally recognizable indication of interesting conditions, was dissected. Internal anatomy of additional samples from each lot that became available also was studied. Characters, such as location of the first dorsal pore and of the genital markings, were determined for every individual of small lots and from random samples (varying in size) of longer series. Divergence or variation from normal in the anatomy was noted in laboratory records without numbering normal specimens or conditions that were seen. Normal or usual seemed to be the same everywhere. Deviation from normal or usual, whenever material was sufficient to permit judgment, always seemed to be similar. *P. hawayana* is exotic in the regions from which all of the material was obtained. Comparison

with worms from the original home of the species, believed to be somewhere in China, has been impossible. Nothing is known about the variation of *hawayana* in its presumed native place.

Significant variation, with respect to some of the most important characters by which pheretimas have been keyed and defined, was found in a number of specimens with no probability of parthenogenesis being involved. Whether any species actually were erected on such variant specimens remains to be learned.

Most species of megadrile oligochaetes are "typological" or "museum" taxa. Some must remain in that condition until such time as arrangements can be made somewhere in the world for extended systematic research on a long-neglected group. Less excusable is the state of our knowledge about many common and widely distributed species. What those zoologists, primarily interested in identifications, did, with the many specimens they must have had that diverged in major ways from the type or that differed significantly from the original description, probably will remain unknown. The wastebasket answer, so often suggested by the skeptic, does precisely state the fate of admittedly unidentified material. Of greater importance may have been the divergent or aberrant individuals that were identified, perhaps erroneously, without characterization, comment, or explanation.

Attention already has been called (Gates, 1960, p. 278) to the importance for megadrile systematics of anomalous, aberrant (including those that may be induced by or result from parasitism and parthenogenesis) and regenerative variations.

LITERATURE CITED

- GATES, G. E. 1960. On Burmese earthworms of the family Megasclecididae. *Bull. Mus. Comp. Zool. Harvard College*, 123: 203-282.